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1969

Reprinted from
Brain Research
Elsevier Publishing Company, Amsterdam
Printed in the Netherlands

CENTRAL INTEGRATION OF VISUAL HALF-FIELDS IN SPLIT-BRAIN MONKEYS

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(Accepted March 17th, 1969)

INTRODUCTION

It has been observed repeatedly that monkeys or cats with the optic chiasm, anterior commissure, and corpus callosum severed cannot transfer a visual pattern discrimination learned with one eye to the other eye. A split-brain cat or monkey which has been trained to select one of two patterns with one eye occluded shows no 'savings' when it is tested with the other eye. In the absence of the forebrain commissures the two hemispheres function independently to a large degree[6].

In other tests for cross integration the sensory information is presented partially to one of the two hemispheres and partially to the other so that the animal must integrate the information in the two hemispheres in order to perform the task.

Trevarthen[8–10] has reported that split-brain monkeys appear to be able to perform interhemispheric size, color, and certain kinds of pattern comparisons in this kind of experiment. Robinson and Voneida[5] found that split-brain cats could eventually perform a comparative brightness task after long retraining. Lee-Teng and Sperry[4] found that stereognostic size information (distinguishing the larger of two cylinders using the two paws) could *not* be cross-matched by split-brain monkeys and questioned previous conclusions based on cross comparison tests. Hamilton *et al.*[2] found that split-brain monkeys could not cross-match for colors presented to right and left eyes.

In an exploratory experiment Sperry and Green[7] studied central integration of patterns in split-brain monkeys. Superimposed half circles were polarized and viewed by the monkey through polarized lenses so that a full circle (the correct choice) could only be perceived when the monkey integrated the half circle patterns going independently to each eye-hemisphere. It was reported that a control monkey with only the chiasm sectioned recovered quickly the ability to perform correctly while 2 of 3 split-brain monkeys could not recover the ability to do the problem. However, these findings should be qualified by the fact that a rather short test of relearning was used.

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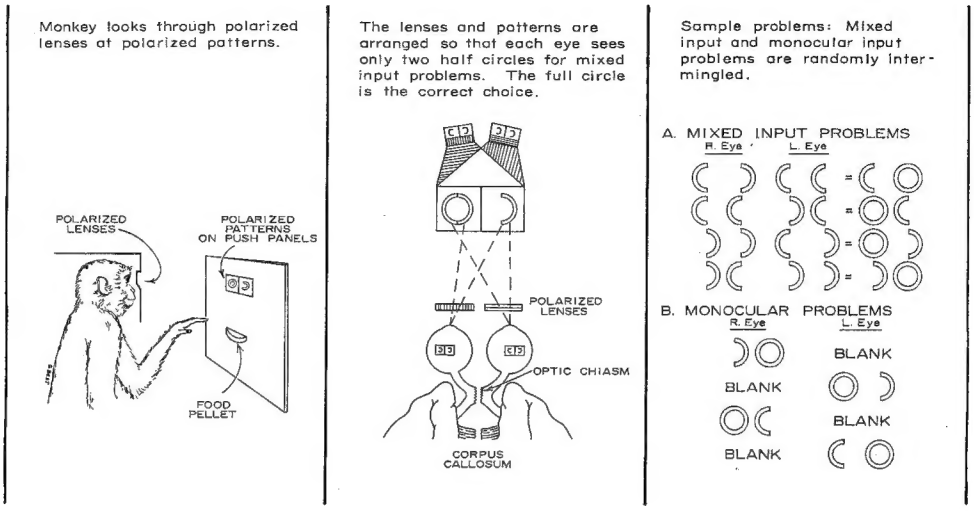

Fig. 1. Experimental design: central integration of visual half-fields.

METHOD

In the present study, the circle–half-circle problem of Sperry and Green was tested in 4 monkeys (*Macaca nemestrina*). Extensive retraining was done on the monkeys so that any possible reintegration could be observed. The forebrain commissures were severed in stages as an aid in evaluating the relative contribution of the different commissures. The animals were first trained as normals and then tested for their ability to do the task after surgical intervention. On each trial, each hemisphere saw 2 half circles. If a central integration took place, the monkey could observe that one pair of half circles projected to form a full circle and the other pair were exactly superimposed to form a half circle (see Fig. 1). Two subsets of problems were randomly intermingled. In 1 subset of 10 problems, all of the patterns — both full-circle and half-circle — went to one eye — either the left or the right (monocular problems). In the second subset of 10 problems a full circle was formed by 2 half circles which were polarized to enter the two eyes separately. (Samples of the 2 types of problems are shown in Fig. 1.) In effect, each monkey observed a repetitive series of 20 full-circle–half-circle problems; he had no way of knowing whether his next problem would be one that could be solved monocularly or one that required integration of the information going to the two eyes. The series was carefully constructed to control for position of the correct screen. The problem was completely automated with Foringer equipment.

As a first step in the experiment, each animal was trained to do the problem as a normal, intact monkey. All animals were maintained on full feeding schedules; during pretraining they were all on a continuous reinforcement schedule so that each correct response was rewarded with a cereal pellet or candy. The series advanced

to the next trial only when the monkey performed correctly on the preceding trial. Three animals had left-handed preferences and the 4th had a right-hand preference. No attempt was made to equalize the use of the two hands.

All of the animals received 500 or more postcriterion trials to assure that they were running at a stable and high rate of accuracy. After the animals were performing well, a series of tests was run to make sure that they had not learned a sequence and that they could not perform the interhemispheric task with one eye alone. The animals were run with first one eye masked and then the other. This provided evidence on whether or not incidental cues existed that would permit the animal to learn the mixed input problems with the information received by only one eye. Following this, each animal was operated on in successive stages. The optic chiasm, anterior commissure and portions of the corpus callosum were sectioned in various combinations in an attempt to determine the precise role of these interhemispheric fibers in integrating the pattern information going to the visual half fields. Testing was begun on all animals within 2 weeks after surgery. Trials to criterion were tallied for all animals at each stage of the operation. Trials were counted correct or incorrect depending on the animal's first response; perseverative errors in the same problem were not counted as additional errors. This eliminates artifactual above chance performance due to the 'win-stay, lose-shift' strategy described by Hamilton *et al.*[2].

RESULTS

Trials to criterion for all of the animals are summarized in Table I. The results for the individual animals are described below.

Aris. This animal was pretrained on the problem as a normal and then operated on in stages. He required 580 trials to learn the mixed input problems as a normal animal and 960 trials to learn the monocular problem. This gave us an estimate of the base line variation in performance on the 2 types of problems for the unoperated animal. Criterion was designated as 90% correct over a run of 60 trials. His learning curve was the traditional negatively accelerated curve that is usually seen for a two-choice discrimination problem. The monocular problems were somewhat more difficult for this animal than the mixed. The animal was tested on an alternate schedule of the same 20 problems in a new sequence and gave no evidence of having learned a sequence. As a control, the monkey was run with his right eye masked; the animal's score on mixed input problems promptly dropped to 51% (or chance level), while his performance on the appropriate monocular problems stayed at 99%. With his left eye masked, similar results were obtained. This demonstrated that the monkey could not perform the task with one eye alone. This control was repeated in all of the monkeys at various stages of learning.

After sectioning of the anterior commissure and the optic chiasm, the monkey required several thousand trials to recover performance on the mixed input problems (4460 — see Table I and Fig. 2). His performance on the monocular problems recovered almost immediately. A control alternative schedule was introduced to be certain the animal had not learned a sequence. A 2:1 ratio reinforcement schedule

TABLE I

TRIALS TO CRITERION FOR MIXED INPUT AND MONOCULAR INPUT PROBLEMS

Criterion = 90% over a run of 60 trials. Training was begun on all animals within 2 weeks after surgery. Days or weeks to criterion on mixed input problems are listed in parentheses.

	Aristotle	*Plato*	*Phidias*	*Marianne*
Pre-op	Mix 580 Mon 960	Mix 500 Mon 480	Mix 300 Mon 180	Mix 460 Mon 260
Optic chiasm		Mix 4360 Mon 100 (4 weeks)	Mix 4420 Mon 180 (4 weeks)	
Optic chiasm plus anterior commissure	Mix 4460 Mon 260 (6 weeks)			
Optic chiasm plus posterior 1/3 corpus callosum		Mix 120 Mon 60 No performance deficit after criterion (1 day)		
Optic chiasm plus anterior commissure plus anterior 2/3 corpus callosum			Mix 420 Mon 80 (1 day)	Mix 6020 Mon 100 (6 weeks)
Optic chiasm plus anterior commissure plus posterior 1/3 of corpus callosum	Mix 1820 Mon 60 Performance deficit observed after criterion (2 weeks)			
Optic chiasm plus anterior commissure plus all of corpus callosum	Mix 4160 Mon 60 Performance deficit observed after criterion (6 weeks)		Mix 5640 Mon 60 Performance deficit observed after criterion (2 weeks)	Mix 60 Mon 60 Performance deficit observed after criterion (1 day)

was used to increase his motivation. After several trials of overtraining his performance on the mixed input problems was virtually indistinguishable from his performance on the monocular problems. An analysis of specific errors suggested that some of the problems were slightly more difficult to scan than others. Some of the slow improvement in mixed input performance may have reflected an underlying learning to scan.

The posterior one-third of the corpus callosum was then sectioned. The animal was able to reach criterion again but even after long overtraining a small but persistent deficit in his performance remained. The range of his best performance on mixed input problems was 85–95%. On the monocular problems he recovered im-

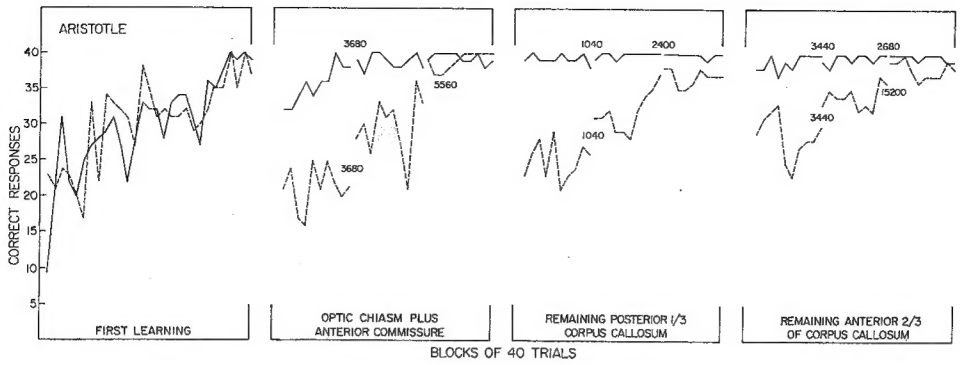

Fig. 2. A comparison of performance on mixed input (dotted lines) and monocular performance (solid lines) after successive transection of forebrain commissures. (Aris) Numbers signify additional trials at indicated points on the graphs.

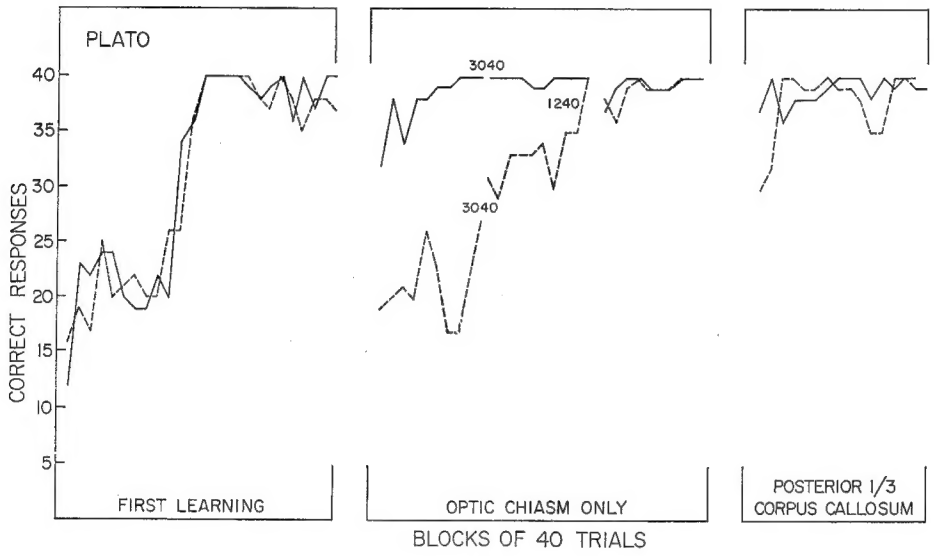

Fig. 3. Mixed input performance (dotted lines) *versus* monocular performance (solid lines) after successive transection of midbrain commissures. (Pla) Numbers signify additional trials at indicated points on the graphs.

mediately to a 90–100% performance. Finally the remainder of the corpus callosum was sectioned. The animal again showed a long slow recovery and never reached the high stable level of his monocular problems. His best performance on mixed problems varied from 80 to 100% with a median value of about 95%. A standard test for transfer of learning was done on the monkey who was now a complete forebrain split. The results were as one would expect. He showed no evidence of interocular transfer of training. It took him 400 trials to learn a two-choice pattern discrimination problem with the left eye and 560 trials to relearn the problem with the right eye.

Pla. This monkey was first trained as a normal (see Table I and Fig. 3). Monocular problems were slightly more difficult than mixed. He was checked on an alternative schedule of problems and gave no evidence of having learned a sequence. He was tested with one eye only as a control; he gave no evidence of being able to choose the correct mixed input pattern unless he could use both eyes. Following this, the optic chiasm was sectioned. The animal showed almost immediate recovery (100 trials) of criterion performance on the monocular problems. After several thousand trials (4360) (some of them on ratio reinforcement schedules) he recovered performance on the mixed input problems as well. The animal showed marked improvement when switched to a more demanding schedule of reinforcement. The monkey was operated on again and the posterior one-third of the corpus callosum was sectioned. Following the operation, the animal showed no loss of his high performance on the monocular problems and a quick recovery on the mixed input problems. Further operations on this animal were not possible because of the development of a postoperative cranial infection.

Phid. This animal was first trained on a simple circle-plus discrimination and then trained on the circle–half-circle problem. He reached criterion performance in only 300 mixed input and 180 monocular trials (see Table I and Fig. 4). The monkey maintained his performance when an alternate schedule of problems was used. He was then tested with one eye masked and his performance dropped to chance level at 45 and 55% on mixed input problems for the right eye and left eye respectively. After this animal's preoperative performance was stabilized, his optic chiasm was sectioned. Eventually he regained the ability to perform both kinds of problems (see Table I). After a few thousand additional postcriterion trials his performance reached the same level on the mixed problems as on the monocular problems. (The section selected for the graph in Fig. 4 shows a slight deficit but this did not persist after the next operation). Following stabilization of criterion performance, the monkey was operated on again and the anterior commissure plus the anterior two-thirds of the corpus callosum was

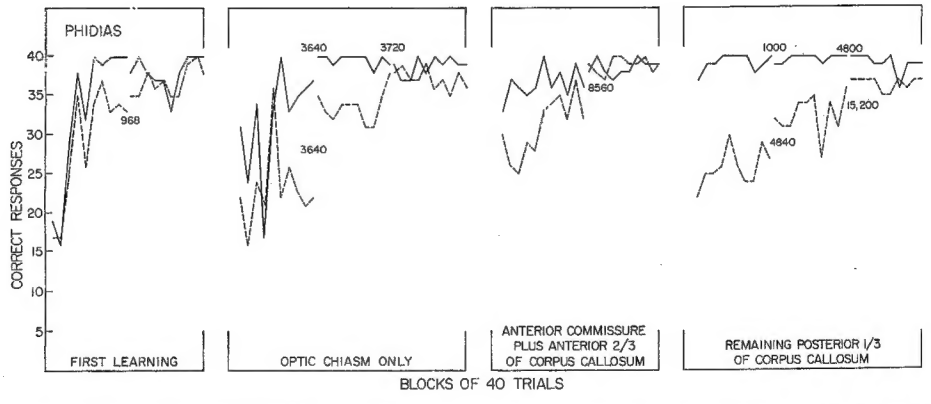

Fig. 4. Mixed input performance (dotted lines) *versus* monocular performance (solid lines) after successive transection of midbrain commissures. (Phid) Numbers signify additional trials at indicated points on the graphs.

sectioned. He recovered rapidly and reached about the same high level of performance on both the monocular and mixed input problems. Finally, the remaining one-third of the corpus callosum was sectioned. As in the other monkeys, a small persistent deficit in performance on the mixed input problems resulted. Even after several thousand postcriterion trials, his performance on the mixed input problems never reached the same high level as on his monocular problems. His best performance in mixed input problems ranged from 80 to 95%. By contrast, his performance on the monocular problems varied between 95 and 100%. This animal was tested on two transfer problems. On the first, his score suggested the possibility of savings (220 trials on the first eye and 120 on the second) but on a second transfer test there was no indication of savings (120 *vs.* 160 trials).

Mari. This animal learned the mixed problem in 460 trials as a normal; monocular problems required only 260 trials. After she was performing well, the optic chiasm, anterior commissure and anterior two-thirds of the corpus callosum were sectioned. The animal showed a long, slow recovery to pre-op performance levels. However, during postcriterion trials, her performance reached the same high level on mixed problems as it did on monocular problems; the two curves were indistinguishable (see Table I and Fig. 5).

Sectioning the remaining one-third of the corpus callosum had no effect on the animal's performance on the monocular problems. On the mixed input problems her performance became more variable and slightly less accurate. Her scores ranged from 80 to 95% (blocks of 40 trials) and a small but consistent deficit of about 5% remained. Her performance on the mixed input problems reached criterion but never quite

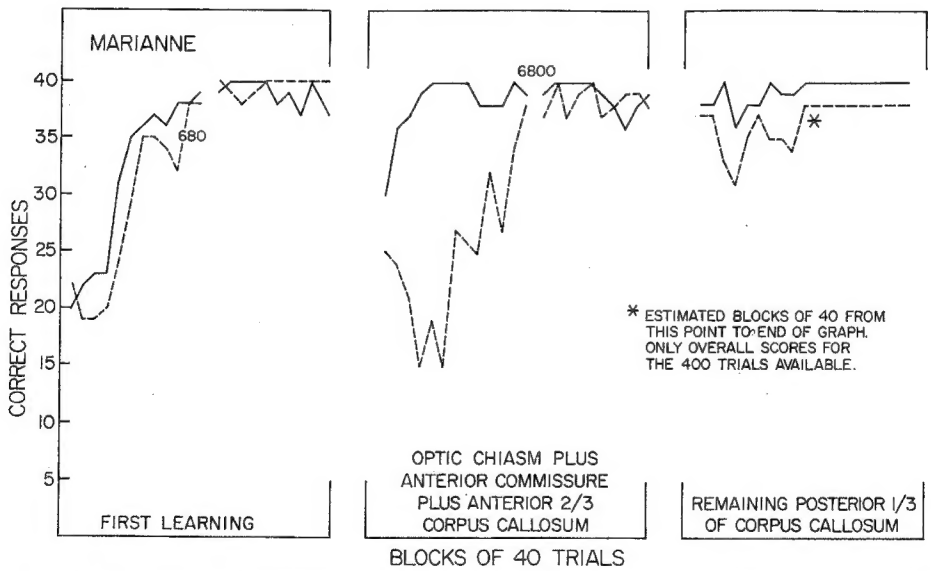

Fig. 5. Mixed input performance (dotted lines) *versus* monocular performance (solid lines) after successive transection of midbrain commissures. (Mari) Numbers signify additional trials at indicated points on the graphs.

matched her performance on the monocular problems. The animal was tested for interocular transfer of discrimination training on a swastika-square problem and showed no savings. It took her slightly longer (2240 trials) to reach criterion with the second eye than with the first (960).

The results for this animal were similar to those for Aris. and Phid.; although retraining was possible, a small but persistent deficit followed sectioning of the posterior one-third of the corpus callosum.

DISCUSSION

The results indicate that monkeys with midline section of the optic chiasm and all neocortical commissures were able to achieve a cross-integration of visual pattern information projected separately to right and left sides although the same animals failed to show interocular transfer of visual pattern training. With two pairs of half circles projected into each hemisphere, the animals were apparently able to discriminate the right-left pair that combined to form in visual space a full-circle from the pair that superimposed to form a half circle. Controls were introduced into the experiment to rule out possibile monocular strategies for performing the cross-integration task. Very long retraining was done when necessary.

The posterior portion of the corpus callosum seemed to improve performance of the task when it was left intact, but it was possible for the monkeys to achieve integration without it. After severing the posterior third of the corpus callosum, monkeys behaved as though they were clumsy at performing a task that they knew how to do. It is possible that the posterior portion of the corpus callosum is especially important in visual guidance of the motor response of the task.

Lee-Teng and Sperry[4] found that split-brain monkeys could not cross-match an intermanual stereognostic size discrimination task that depended upon the animal touching and manipulating small wooden cylinders. Hamilton *et al.*[2] have reported that split-brain monkeys cannot cross-match colors. Trevarthen[10] claims that split-brain monkeys can select the larger of two circles presented separately to the two hemispheres, although '... a bilateral comparison of the orientation of a black bar and a striped foreground is impossible.' (p. 327). Trevarthen[10] distinguishes between foveal visual tasks which are mediated strictly by the cortex and ambient visual tasks which may be mediated by cortico-subhemispheric visual processes.

The mechanisms mediating integration of the visual half-fields in the present study remain to be discovered. One of our colleagues (R.T. Kado) has pointed out that it is conceivable that a central integration of the super-position of the (wrong) half-circle pattern took place so that the wrong pattern appeared brighter than the correct pattern. It is possible that tegumental or collicular pathways mediate the integration. The very long overtraining of the motor response may make a cerebellar integration possible.

The present results suggest that some form or other of non-cortical mediation of visual pattern information is possible under the conditions of the integration experiment. Nevertheless, 2 of the 3 split-brain monkeys (Phid. showed equivocal

results) performed as expected on tests of interocular transfer, *i.e.*, they did not transfer. This suggests that there are some functional aspects to the transfer task which block the relaying of visual pattern information from one half-brain to the other, or which prevent relayed information being utilized or 'expressed' by the animal.

We can speculate briefly about what these functional aspects might be. One may argue that in the transfer task the whole learned visuo-motor task (the engram) is lateralized in one hemisphere. In the integration task it is only the visual pattern information *per se* which is directed independently to the two hemispheres. The one hemisphere learning of the transfer task may be the special feature that prevents the relaying of the engram to the second hemisphere.

Secondly, it is possible that in the transfer task the animal is less well motivated since increased ratios of reinforcement and extraordinarily long retraining were done in the integration task. If motivation is an important factor, one may consider whether or not the engram is 'available' in the second hemisphere during transfer studies — but not used.

Thirdly, active inhibition of second hemisphere learning may be occurring in the transfer of training tests. In the integrative task there is no opportunity for such inhibition to occur, since both hemispheres must be repeatedly consulted in order for the animal to make the correct motor choice. Sherrington, and later Pavlov, suggested that utilizing very specific pathways may inhibit the development of new relay paths in the same experimental situation; for example, Koslovskaya[3] has shown that dogs trained to perform a very precise visuo-motor skill have great difficulty in acquiring a new visuo-motor skill in the same situation. If it were true that active inhibition played a role in the transfer task, one would expect that an incompletely trained split-brain animal would show more transfer than one trained to a high criterion or over-trained. There is little evidence available. However, Hamilton and Gazzaniga[1] have reported that a split-brain monkey trained to an 85% level of accuracy with one eye (a color discrimination task) does, in fact, show more transfer than a split-brain monkey who has been overtrained in the same task. In the integrative task the pathways are complex, but there is no opportunity for active inhibition to interfere with the animal's performance. It should be added that we have no way of knowing, at present, if active inhibition might affect only motor performance or storage of information or both.

SUMMARY

Tests on split-brain animals have suggested that visual information relayed to one eye, and presumably to one hemisphere, is not available to the second hemisphere. The present study was designed to attempt to force the split-brain monkey to integrate visual pattern information across the two hemispheres. A circle and half circle were presented to the monkey through a system of polarized lights and lenses so that each eye saw only two half circles. In order for the animal to be consistently rewarded, he had to select the panel on which a projected full circle was formed. Four monkeys (*Macaca nemestrina*) were trained as normals and operated on successively (optic

chiasm and forebrain commissures). All of the animals eventually relearned the task. A small but persistent deficit in postcriterion performance was observed after the posterior third of the corpus callosum was cut, following earlier transection of the chiasm, anterior commissure and anterior two-thirds of the corpus callosum. Possible mediating mechanisms for such central integration are mentioned.

ACKNOWLEDGEMENTS

This investigation was supported by the National Institute of Mental Health (Grant MH 03372) of the U.S. Public Health Service and by Space Biology, UCLA (NASA NsG 237–62).

We are indebted to Lois MacBird for assistance in surgery; appreciation is expressed to Miss MacBird and Eef Goedemans for most of the handling and training of the monkeys.

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